



Review

Functional traits explaining plant responses to past and future climate changes^{*}

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ABSTRACT

Climate change (“global warming”) is expected to exert serious negative effects on biodiversity. Knowledge and understanding of non-anthropogenic climate changes in previous geological eras may improve predictions about ongoing trends. In this context plant functional traits can be useful tools – the ecotype variations and plasticity of morphological, physiological and developmental traits may help to determine which plants or plant groups might overcome present severely and rapidly changing environmental conditions. The mechanisms behind these trait–environment relationships will be relevant e.g. for a more realistic modelling of biogeochemical cycles and species distributions.

In this Special Issue topics addressed above will be discussed in detail, grouped into the following sections: (1) Paleoclimate and paleovegetation, (2) Plant Silica and phytoliths, (3) Environmental gradients and intraspecific trait variation, (4) Experimental approaches to test effects of climate change on plant performance and functional traits, (5) Selection of traits – from empirical correlations to mechanistic responses, (6) Responses of plant functional traits and vegetation to global warming. Perspectives for future research on functional plant traits – climate change are discussed for following fields: (i) Clear definition of relevant climate parameters, (ii) a more mechanistic approach for functional plant traits, (iii) intraspecific trait variation, (iv) plant functional traits with respect to disturbances, (v) transplant experiments using whole communities including soil environment, (vi) remote sensing (hyperspectral and LIDAR), (vii) more realistic approaches in vegetation modelling.

1. Introduction

Already at the beginning of the 19th century, after the establishment of the hierarchical classification of plant and animal species in a biological system by C. Linnaeus, first attempts for a functional classification of plants were started by A. von Humboldt in his “Ideen zu einer Physiognomie der Gewächse” (“Ideas for a Physiognomy of Plants”; Humboldt, 1806). Based on a variety of characteristics, he assigned the huge diversity of plant species which he had seen mainly during his voyage to South America to 18 different forms, among them palms, heather form, succulents, needle-leaved plants (gymnosperms), lianas, grasses, ferns, willow form and laurel form. Humboldt postulated temperature to be the major reason behind all these forms, leading to convergence in plant characteristics and forms. One hundred years later, Schimper (1903) combined plant physiology and ecology in order to explain the effects of environmental conditions on plant performance and distribution, i.e. plant adaptation in different vegetation zones and types. It took ecologists again nearly a century to develop theoretical

concepts on the relationship between characteristics of plants and their environment, after the seminal experiments by Phil Grime on “comparative ecology of flowering plants” in the middle of the 20th century (Grime, 1965). After “functional ecology” being defined by Calow (1987), “functional traits” were increasingly applied in plant ecology, not only for classification and grouping of organisms by their function, but more and more to investigate trait–environment relationships in order to explain resource economics and stress resistance mechanisms of plants, finally answering the old question “Where is a plant growing, and why?”. In the following, functional traits have been used for a multitude of purposes in organismic biology (ecophysiology, evolutionary ecology), community ecology (functional diversity, assembly rules) and ecosystem analysis (species effects e.g. on biogeochemical cycles and ecosystem services) and in global vegetation modelling (cf. Weiher et al., 1999; Violle et al., 2007; Shipley et al., 2016). This caused ambiguous definitions and use of the trait concept, which was finally solved by Violle et al. (2007): “a trait is any morphological, physiological or phenological feature measurable at the individual

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level, from the cell to the whole-organism level, without reference to the environment or any other level of organization.”

In view of global change, functional traits are a non-dispensable tool to predict responses of plants and vegetation to environmental drivers like global warming, land use change or invasive species, and the effects of these drivers on community structure and ecosystem functions (Lavorel and Garnier, 2002). In this context, Lavorel and Garnier (2002) coined the terms “response traits” and “effect traits”. However, there is some overlap between response and effect traits, partly due to indirect linkages like trade-offs or character association due to third factors (Lavorel and Garnier, 2002).

When studying trait–environment relationships, the question arises which functional traits should be selected as relevant ones (Weiher et al., 1999; Funk et al., 2016). In a first synthetic attempt on key chemical, structural and physiological leaf traits, Wright et al. (2004) elaborated a dichotomy between quick return versus slow return on investment of resources, the so-called “leaf economic spectrum” (LES). The key leaf traits such as leaf mass per area (LMA), photosynthetic assimilation rate, leaf nitrogen content (LNC), leaf phosphorus content (LPC) or leaf lifespan were found to be coordinated across major plant functional types, growth forms and biomes, with a small influence of climate only. This concept was extended by Reich (2014) to the whole-plant level, including stem traits such as hydraulic conductivity or wood density, and traits of fine roots (e.g. hydraulic conductivity, specific root length, longevity, mycorrhiza). Again, relationships between economic traits and climate (temperature or precipitation gradients) explained a small proportion of total variance only. Rather traits involved in carbon, nutrient and water economy vary in a coordinated way both within and among leaves, stem and root systems, with environment and evolutionary history. Díaz et al. (2016), including traits also relevant to reproduction (cf. the leaf–height–seed strategy scheme by Westoby, 1998) were successful in reducing their initial six-dimensional trait space (adult plant height, stem specific density, leaf area, LMA, LNC, diaspore mass) to a two-dimensional global spectrum, with one dimension reflecting plant size, the second dimension leaf economics.

All these global analyses are based on mean values for plant functional traits, neglecting intraspecific trait variation (ITV). Violle et al. (2012) re-introduced the basic concept of the theory of evolution by natural selection by Darwin and Wallace in traits and community ecology and emphasized the importance of ITV for a number of ecological and evolutionary processes. Functional diversity of species within a community can be decreased through effects of abiotic conditions (“abiotic filtering”) or increased through biotic interactions (“limiting similarity”; Albert et al., 2012). Although the relevance of ITV has been questioned again by Shipley et al. (2016); Siefert et al. (2015) have emphasized its role for environmental changes (slow, but broad in scope for heritable genetic differences; fast, but with a limited scope for plastic trait responses).

One major component of global change is climate change (“global warming”), causing serious negative effects for biodiversity (Sala et al., 2000), with a most tremendous risk for microendemics (Bitencourt et al., 2016). Generally, shifts in plant species to be expected for the future will affect community structure and assemblages, and finally ecosystem functions and services. On the other hand, there have been major non-anthropogenic climate changes in previous geological eras. Their knowledge and understanding may improve predictions about ongoing trends through statistical modelling and enhance our capacity for management to keep ecosystems as intact as possible and reduce harmful impacts of current climate change. In this context plant functional traits can be useful tools – the ecotype variations and plasticity of morphological, physiological and developmental traits may help to determine which plants or plant groups might overcome present severely and rapidly changing environmental conditions. The mechanisms behind these trait–environment relationships will be relevant e.g. for a more realistic modelling of biogeochemical cycles and species

distributions.

In this Special Issue on *Functional Traits Explaining Plant Responses to Past and Future Climate Changes* (Flora 254C, 2019) papers have been compiled on the following topics:

- morphological and anatomical plant traits as evidence of past climate changes
- variation of morphological and physiological traits along environmental gradients, between ecotypes and due to different experimental treatment conditions simulating past, present and future environmental conditions due to climate change
- assessment of predictors for plant performance and survival under past and future climate (changes).

In the following topics addressed above will be discussed in more detail, based on the publications in this Special Issue, put into context with recent relevant publications in the same field. These topics are grouped into the following sections: (1) Paleoclimate and paleovegetation, (2) Plant Silica and phytoliths, (3) Environmental gradients and intraspecific trait variation, (4) Experimental approaches to test effects of climate change on plant performance and functional traits, (5) Selection of traits – from empirical correlations to mechanistic responses, (6) Responses of plant functional traits and vegetation to global warming.

2. Paleoclimate and paleovegetation

The use of plant functional traits to characterize paleoclimate is based on the assumption that paleotraits can be calibrated against similar traits from extant vegetation with an established trait–environment relationship, although a clear causal explanation is mostly lacking and traits are usually influenced by several, often interacting environmental parameters. Most relevant in the context of this Special Issue are leaf traits such as leaf margin (presence / absence of teeth) and area. Due to the clear negative relationship between proportion of taxa with toothed leaves and mean annual temperature (MAT) this trait is widely used in paleoecology (Roth-Nebelsick et al., 2017). According to Gillison (2019a), in this Special Issue, the functional relevance of leaf teeth is well proven, and they confer adaptive value particularly for deciduous leaves (Roth-Nebelsick et al., 2017). However, as Gillison (2019a) emphasizes, leaf margin analysis has been criticized for several reasons, e.g. imprecise temperature calibration when using leaf margin attributes of extant taxa, taphonomic bias, missing consideration of additional leaf traits such as area and thickness, local site conditions (e.g. dry versus wet soils) and phylogenetic disparities between study regions. However, Kunzmann et al. (2018), in this Special Issue, compared different methods beyond leaf margin analysis, based on a large set of leaf physiognomic characters and taxonomical composition of the fossil flora, yielding in similar estimates of the paleoclimate for a Paleogene ecosystem in Central Germany.

Although leaf area has been widely used as an indicator for paleo-temperature Gillison (2019a), due to confounding with water availability the positive relationship between leaf size and temperature is weak only (Roth-Nebelsick et al., 2017). The relationship between leaf area and temperature is physically mediated by the thickness of the leaf boundary layer, which, however, can be modulated by leaf shape (length/width ratio, lobes etc.; Roth-Nebelsick and Konrad, 2018). Another morpho-anatomical leaf trait – leaf venation –, being denser in small compared to large leaves, can be used as an indicator of drought resistance due to lesser susceptibility to leaf vein embolism in small leaves (Sack and Scoffoni, 2013). Thus density of leaf veins, affecting leaf hydraulic conductance, is higher in species from dry compared to wet habitats, in sun leaves higher than in shade leaves, and in trees higher than in herbs (Roth-Nebelsick et al., 2017). Furthermore, leaf inclination can modify the relation between leaf size and temperature, as well as leaf position within the canopy, the occurrence of a frost-free

period for evergreen angiosperm leaves, atmospheric CO₂ concentration (Temme et al., 2015), or nutrient availability, representing serious obstacles in using leaf size for estimates of paleoclimates (see Gillison (2019a)).

Therefore, Gillison (2019a) recommends the combination of leaf size with other functional traits, such as derived from a modal plant functional type syndrome (see Gillison, 2019b). Following this line, Roth-Nebelsick et al. (2017) used leaf mass per area (LMA) as assessed by an empirical correlation between leaf area, leaf mass and petiole width measured on fossil leaf material as an additional predictor for paleoclimatic research. Leaf mass per area is positively correlated with leaf life span (e.g. Mediavilla et al., 2008). However, on a global scale there is no clear relationship to climate parameters such as MAT, due to effects of nutrient availability with consequences on evergreen versus deciduous leaf habit (see also Gillison, 2019a). However, in combination with leaf venation patterns, Roth-Nebelsick et al. (2017) found evidence for a warm and equable climate in late Eocene of Central Europe, with a prevalence of evergreen plants displaying high LMA leaves, and a transition to a decreasing growing season length, with lower temperature and humidity, documented by an increasing frequency of large and lobed leaves with a low LMA, indicating shorter leaf life span, e.g. due to dry seasons and / or (mild) winters. Thus through the combination of fossil leaf architecture and a trait from the LES, authors could not only infer on past climates and ecosystems, but also contribute to our understanding of the evolution of leaf functional traits during the Paleogene.

Using only LMA, as inferred from fossil leaf cuticles on the basis of a close relationship between cuticle thickness and LMA for extant gymnosperms, Soh et al. (2017) could show shifts from low-LMA taxa in Late Triassic forests to high-LMA taxa in Early Jurassic forests of East Greenland, probably due to global warming induced by extremely high atmospheric CO₂ concentrations. Nevertheless, as emphasized by Gillison (2019a), the uncertainties in the assessment of paleovegetation, due to e.g. taphonomic bias, delineation of local paleohabitats and limited data sets, do not allow a valid reconstruction of past communities – the relevant scale for structuring assemblages of plants as based on their functional traits and their relationship with environmental factors such as climate. Furthermore, the “classical” parameters leaf size, shape and margin have been investigated for biomes dominated by woody dicots, much less for herbaceous species (forbs and grasses).

On the other hand, Roth-Nebelsick and Konrad (2018), in this Special Issue, applying leaf gas exchange modelling based on leaf biochemistry and gas diffusion and using parameters both from extant and fossil leaves, coupled with heat transfer as dependent on leaf size, could elegantly demonstrate only minor effects of elevated CO₂ concentrations on leaf temperature under non-limiting water supply. Thus atmospheric CO₂ concentrations only marginally affect the correlation of leaf size with environmental (e.g. climatic) parameters (at least under sufficient water supply) – reinforcing convictions that responses of leaf traits to the environment cannot only be explained by causal mechanisms for extant vegetation but also be used for extrapolation to paleoclimates and future climate scenarios. This approach, based on an ecophysiological analysis of leaf traits, may be particularly useful in view of non-analogue climate situations with a constellation of abiotic environmental parameters which do not exist today.

3. Plant silica and phytoliths

Among the extensive list of plant functional traits discussed by Gillison (2019a) as indicators for paleovegetation, the author stresses the suitability of phytoliths to detect past vegetation changes and derive hypotheses on paleoclimates. Phytoliths are microscopic particles of opaline silica (Si) occurring in a large number of morphotypes in a given plant species. Based on their presence or absence and their abundance, they can be used for diagnosing plant taxa from the family down to the species level. They have been repeatedly used as

environmental indicator proxies (e.g. Katz et al., 2013; Dey et al., 2015; Issaharou-Matchi et al., 2016; Li et al., 2018a). In this Special Issue, Mukherjee et al. (2018) present a first example on the use of phytoliths from pteridophytes and their interrelationships with climate patterns along elevational gradients. Authors found evidence that temperature, actual evapotranspiration and moisture affect phytolith spectra in pteridophytes, with different morphotypes collected from tropical, subtropical and temperate elevation zones in the eastern Himalaya. Thus they could differentiate various vegetation zones along their elevational gradient, with changing climatic parameters including a complex interaction of water availability and evapotranspiration, based on phytolith spectra of pteridophytes.

Katz (2018), in this Special Issue, based on a number of examples on the role of plant Si in stress adaptation (e.g. participation in stomatal regulation) and in ecosystems (e.g. carbon cycle, herbivory; Si:C trade-offs), claims plant Si content to be a functional trait. Due to its link between plant responses to the environment and effects on community and ecosystem properties a better understanding of the mechanisms behind these functions and interactions with other plant functional traits and of the variation of plant Si contents in response to environmental factors including intraspecific variations may improve the predictive power when modelling effects of climate change on ecosystem structure and functions.

4. Environmental gradients and intraspecific trait variation

4.1. Environmental gradients at global, continental and regional scales

Environmental gradients of abiotic (particularly climatic) factors along large geographic (latitudinal, elevational) scales affect via evolutionary, biogeographic and ecological processes (e.g. environmental filtering) distribution of plant species and plant traits in space and time. Therefore, these environmental gradients have already been used for a long time to study the distribution of plant species and vegetation types, and the underlying responses of functional traits e.g. to temperature and precipitation (Humboldt, 1806; Schimper, 1903). Following the concept of the leaf economic spectrum (LES) with distribution of plant traits along climatic gradients at a global scale including many biomes and plant growth forms (Wright et al., 2004), research focused on variation of functional traits of plant species as linked to environmental factors, with co-occurring species displaying trait differentiation due to biotic interactions, mainly interspecific competition (niche complementarity). Thus trait variation along environmental gradients has largely been analysed on the basis of mean species values, both on a global scale (e.g. Moles et al., 2009) and on regional scales (e.g. Laughlin et al., 2011). Results from these studies have been used for predictions on how individual plant species might respond to global change (Lavorel and Garnier, 2002).

The use of species mean traits has been facilitated by the existence of large plant data bases, e.g. TRY (Kattge et al., 2011) or BIEN (Enquist et al., 2016). Using data on plant distribution and functional traits from these two data bases, Šímová et al. (2018) analysed spatial patterns of community means and their variances for several plant traits related to key ecological strategies from herbaceous and woody species from the New World, and their relationship with climate. Due to a higher diversity in life strategies for herbaceous compared to woody plants, growth form (and phylogeny) strongly affected trait–climate relationships at this continental scale, with temperature seasonality showing often the strongest effect. Based on an analysis of trait variances, the authors found little evidence that harsh environments reduced the scope of successful strategies.

On a regional scale (Taibai Mountain, Central China), Xu et al. (2018) found a similar pattern of trait–habitat relationships for different growth forms (woody and herbaceous species), leaf traits (leaf area, specific leaf area, leaf dry matter content), and plant height along a gradient with increasing habitat severity. This shows the strong effect

of habitat filtering, with low temperatures and low water availability as those factors determining habitat severity. However, trait–trait relationships differed among growth forms, indicating contrasting responses to alterations in climate conditions, which has to be considered in predictions of climate-induced vegetation changes.

For a study at a scale intermediate between regional and continental, Asner et al. (2017) applied both field sampling and airborne remote sensing (RS) for nine landscape units (ca. 1000 ha each) along an elevation gradient from the eastern Andes (3557 m above sea level, a.s.l.) to the low-land Peruvian Amazon (215 m a.s.l.). Assays on leaves collected in the field and of visible-to-shortwave infrared (VSWIR) data from RS imaging which were converted to estimates of canopy foliar traits included LMA, leaf chlorophyll and phosphorus concentration, contents of water (LWC), non-structural carbohydrates (NSC), lignin and phenols. Results from both approaches unanimously showed that LMA, LWC and NSC increased in mean values and variance with elevation, following an environmental gradient of decreasing temperature and drought. Thus this study convincingly demonstrates the applicability of RS technologies for multi-scale approaches in elucidating trait–environment relationships.

A traditional approach in vegetation ecology to characterize environmental conditions is the use of environmental indicators values, e.g. for climate and soil parameters. In a sample of more than 1000 plant species from Northern Italy at the fringe of the Mediterranean Basin, Dalle Fratte et al. (2018), in this Special Issue, investigated the general response of plant traits to environmental factors as characterized by Landolt Environmental Indicators (EIs). Functional traits related to size (canopy height, leaf area) correlated with meso- and microclimatic EIs for temperature and light, whereas traits from the LES (SLA, LNC) correlated with soil EIs for moisture, soil reaction (acidity) and nitrogen. Authors concluded that due to the effect of soil factors on plant functional traits changes in soil fertility e.g. due to land use changes could trigger and magnify responses to climate change in the future.

For the present Special Issue, two latitudinal transects following a precipitation / aridity gradient have been performed in Central Asiatic steppe and desert communities with their strongly continental climate (extreme cold and heat). Beyond “classical” whole-leaf traits like LMA, leaf dry matter content (LDMC) and leaf thickness (LT), Ivanova et al. (2018), in this Special Issue, studied leaf internal structural and physiological parameters such as chloroplast number per leaf area (N_{chl}/A), and total surface area of chloroplasts (A_{chl}/A) and cells (A_{mes}/A), closely related to photosynthetic functioning of C3 plants. The authors found a dominant effect of plant functional type, but low difference between sites along the aridity gradient for the “classical” parameters LT and LMA, whereas mesophyll traits were clearly related to the aridity index. A_{mes}/A and A_{chl}/A , the most important leaf structural parameters related to aridity in this study, characterize leaf internal exchange surfaces for CO_2 within the mesophyll and are therefore an anatomical determinant of mesophyll conductance and thus much better mechanistically related to photosynthetic capacity than LMA which is composed of LDMC, LT and leaf density, and influenced by varying proportions of epidermis, mesophyll, vessels etc. (Garnier et al., 2016; see also Gillison, 2019a).

In a second paper along a precipitation gradient in Central Asia, Lang et al. (2018), in this Special Issue, emphasize intraspecific variation of traits related to aboveground growth, supposed to be strongly affected by moisture availability, in Mongolian rangelands. Trait responses were species-specific, usually with a unimodal pattern, and only rarely related to precipitation. Specific leaf area (SLA) did not show a clear pattern for four out of six study species, neither did photosynthetic performance. Only three traits (canopy height, SLA, maximum quantum yield of photosystem II) of two study species were significantly related to long-term variability of precipitation. Authors concluded that “different functional traits may respond to different environmental factors in a trait-specific and species-specific way” (Lang

et al., 2018).

4.2. Intraspecific trait variation at various scales

Although in the study of trait–environment relationships the emphasis has been on species mean trait values for a long time, based on the assumption that intraspecific trait variation (ITV) can be neglected compared to between-species variability (BTV) (“ITV < BTV assumption”), both empirical evidence (e.g. Albert et al., 2010a, b; Messier et al., 2010) and theoretical concepts of community assembly and evolutionary ecology (Keddy, 1992; Rickleby, 2003) have challenged the ITV < BTV assumption. A major reason for the dispute on ITV versus BTV is to be found in the scale of the investigations: the search for general patterns at the biome and global scale including vegetation modelling has been performed at the interspecific level (e.g. Wright et al., 2004, 2017; Moles et al., 2009, 2014; Reich, 2014; van Bodegom et al., 2014; Díaz et al., 2016), whereas community structure and processes have to be studied at the intraspecific level. ITV is made up of three main components: population-level (ITV_{pop}), between-individual (ITV_{BI}), and within-individual (ITV_{WI}) variability (Albert et al., 2011). Both genetic and environmental (e.g. climatic) factors can cause ITV, the relative contribution of each to be quantified by experiments under controlled conditions (e.g. “common gardens”). In addition, a plant phenotype can also change during its development (i.e. ontogeny).

In a global meta-analysis on the relative extent of ITV in plant communities Siefert et al. (2015) found 25% of total variation within communities and 32% of total among-community variation in mean trait values accounted for by ITV. Intraspecific variation for leaf chemical traits was larger than ITV for morphological traits, both within and among communities. There was a weak trend for the relative extent of ITV to increase with decreasing MAT and mean annual precipitation (MAP). ITV was most relevant for local scales and short environmental gradients. Since the relevance of ITV decreased with species richness, it was more important in species-poor communities.

Useful information on the extent of ITV can be gained from field sampling along environmental gradients. As in the SI paper by Lang et al. (2018), “key” functional traits such as SLA (or its inverse LMA) and other traits based on the LES have usually been recorded along environmental gradients. SLA (respectively LMA) is supposed to be a good indicator for water and nutrient conservation and is related to leaf physiology (e.g. net photosynthesis rate per unit leaf dry mass, A_{mass} ; leaf nitrogen and phosphorus concentration, LNC, LPC). In a study on four species of *Banksia* along a gradient of moisture, temperature and soil nutrients in Western Australia, Cochran et al. (2016) found significant relationships between (i) MAP and LA respectively SLA (negative) or leaf N per area (N_{area} , positive); and (ii) MAT and SLA (negative) and N_{area} (positive). Probably due to the short longitudinal gradient, enabling a high gene flow, intra-specific trait variation was weak or absent or opposite to the general trend. Nevertheless, there was considerable among-population variation in a number of traits, constituting “populations as evolutionary units” with their own specific responsiveness to changing environmental conditions.

Addressing the issue of different scales of ITV (population or site scale with plant trait variation being affected e.g. by climatic factors such as temperature and precipitation; between-individual scale with ITV_{BI} e.g. due to ontogeny, microsite or biotic effects such as intra- and interspecific competition for light, water, nutrients etc.), Li et al. (2018b) used three nested spatial scales (individual, plot, site) to characterize variability in physiological and morphological leaf traits of two dominant trees in a Korean pine–broadleaved forest along broad environmental gradients of climate and soil. Intraspecific variation across spatial scales was not consistent between morphological (SLA, LDMC) and physiological traits (LNC, LPC). Physiological traits of resource-acquisitive (i.e. broadleaved) species were more sensitive to gradients of environmental factors of climate (MAT, MAP) and soil (P concentration). In a similar study, Salazar et al. (2018) investigated

intraspecific variability of leaf functional traits along a climatic gradient in *Prosopis pallida*, a phreatophyte from dry forests in Northern Peru. None of the leaf structural (e.g. LMA, LDMC, stomatal size or density) or leaf physiological traits (e.g. A_{mass} , stomatal conductance g_s , LNC) was related to MAP, probably due to hydraulic lift. This highlights the consideration of life form and resource acquisition mechanisms when establishing trait–environment relationships.

Wigley et al. (2016) emphasize another factor which complicates the relationship between functional traits and plant environment: phylogenetic relatedness. In a study on leaf traits from woody species occurring in African savannas across climate and soil fertility gradients, due to the high proportion of legumes and the important role of herbivory and fire the authors could not find any significant relationship between climate (or soil fertility) and LES traits such as LPC or tensile strength. This shows that drivers like disturbance and herbivory have to be considered as well when interpreting trait–climate relationships.

Accordingly, in a study by Garnier et al. (2018), in this Special Issue, on the variation in traits related to the “global spectrum of plant form and function” (Díaz et al., 2016) between species and populations of species from sites with different drought conditions in the Mediterranean Basin, the nature and level of disturbance (wildfire and grazing) affected the relationship between some plant stature and organ size related traits for low stature species contradicting the expectations from the drought stress gradient. In contrast, leaf morpho-anatomical and chemical traits were more consistent for low and high stature plants and among life forms. Similarly to Lang et al. (2018), SLA tended to be higher (in the case of deciduous phanerophytes) at the arid end of the gradient compared to the centre, probably due to lower leaf thickness. Generally, intraspecific trait variation was lower than interspecific variation. Although the phenotypic space as defined by the “global spectrum” (Díaz et al., 2016) was not modified in response to the drought gradient, the selected traits did not respond clearly to the environmental gradient. Therefore authors suggest to include traits which are more specific to ecophysiological processes and mechanisms – a topic to be discussed later on. Based on their results, Garnier et al. (2018) conclude that response to climate change will be modulated by local environmental factors such as disturbances; nevertheless, more intensive droughts are expected to favour species with a conservative leaf syndrome (i.e. low SLA, LNC, LPC, high LDMC).

Although there was a considerable environmental gradient in the study of Garnier et al. (2018) with a doubling of MAP and aridity index between sites, the geographic distance between sites was rather small. In contrast, Tautenhahn et al. (2019), in this Special Issue, studied ITV for five co-occurring species from dry grasslands over a wide geographical range in Europe covering most of their environmental range, considering both ITV between populations (ITV_{pop}) and ITV within populations (ITV_{BI}). In addition, trait variability was evaluated applying a multivariate approach by n-dimensional hypervolumes (Blonder, 2018). Whereas for the univariate analysis ITV, possibly due to the large geographical range, dominated over BTV for most traits, in the multivariate case ITV accounted for less than a quarter of total trait variability, confirming experience on identification of species via morphological traits and the concept of the ecological niche. ITV_{pop} dominated ITV when considering many traits, indicating the importance of environmental effects on ITV in a multivariate setting. For the water-limited European dry grasslands, MAP was a better predictor for plant traits than MAT or mean annual growing degree days; however, the best trait predictor was growing degree days until day of sampling which suggests that short-term intra-annual plastic responses of plant traits may be relevant for species of European dry grasslands in view of climate change.

This points to a component of intraspecific trait variation, which, apart from heritable genetic variation, phenotypic plasticity and ontogeny, is often neglected – phenology. In a study with three *Cistus* species which produce different leaf cohorts under extended growing seasons in their Mediterranean habitats, Puglielli et al. (2018), in this Special

Issue, found different acclimatisation capacity for leaves produced under different environmental conditions. This had a profound effect on trait co-variation patterns, with a clear shift from a lack of coordination between physiological (photosynthesis per leaf mass) and morphological traits (LMA, leaf thickness, LDMC) for leaves produced in the winter, to significant correlations for leaves produced under more benign conditions during spring. Thus, the different cohorts of leaves are supposed to acclimate their functional traits and also the mutual relationships between traits (co-variation) over the course of a growing season. It can be concluded that under conditions of global warming, with a shift of temperature and precipitation patterns and possibly novel non-analogue constellation of climate parameters, species' capacity to maintain and adjust this acclimatisation capacity may be crucial for their performance and survival.

4.3. Transplant experiments

One way to assess the potential of intraspecific spatial patterns in trait variation to predict plant and community responses to climate change is experimentally manipulating the climatic environment by transplanting individuals or entire communities to new sites differing in climate. Transplanting alpine grassland communities in Southern Norway, Guittar et al. (2016) found support for the space-for-time assumption for traits related to plant architecture such as maximum height, number of dormant meristems or persistence of connections between ramets, but not for traits related to resource-use strategy (LA, SLA), demonstrating the need for choosing ecologically relevant traits, particularly in regions where species with traits from a restricted range of the whole LES or life-form spectrum occur.

Henn et al. (2018) studied the relevance of phenotypic plasticity (i.e. the ability of a genotype to produce different phenotypes under varying environmental conditions) for adaptation to future climate in a reciprocal transplantation experiment across an elevational gradient for alpine species in China. With decreasing mean temperature, conservative traits such as leaf thickness or LDMC increased, whereas traits related to a resource-acquisitive strategy such as LA, LNC or leaf N:P ratio decreased. Intraspecific variation due to genetic factors was high for SLA and low for LA, whereas it was the other way round for phenotypic plasticity with its potential rapid response to environmental changes, e. g. within one growing season.

Working with one plant species (*Oxalis montana*) only, Lajoie and Vellend (2018) in a reciprocal transplanting experiment between three elevations found a dominant role of phenotypic plasticity for ITV and weak local adaptation due to high gene flow in this perennial plant species, and therefore a small role of microevolution in the adaptation to changing environments. Authors concluded that this species shows a limited potential under sustained environmental change and stressed the importance of species turnover (see Section 7).

5. Experimental approaches to test effects of climate change on plant performance and functional traits

Major environmental factors related to climate change are temperature and precipitation, and atmospheric CO₂ concentration as the putative main driver of anthropogenic climate change. In the course of global warming, plants will be subjected more and more to extreme temperatures, particularly heat, often associated with reduced water availability and drought. Experiments under controlled conditions allow to elucidate upper and lower limits of tolerance of plants to high temperatures and water deficits, without the influence of other confounding (micro-)habitat conditions as in observational studies at the species' natural sites. Sastry et al. (2018), in a controlled experiment in the greenhouse with saplings from 12 tree species of seasonally dry tropical forests, investigated the combined effect of high temperature and water deficit on chlorophyll *a* fluorescence as an indicator of photosynthetic thermotolerance, and the relationship between

thermotolerance and functional leaf traits. Thermotolerance was positively related to LMA, and negatively to rates of photosynthesis (PS). Thus vulnerability of the investigated species to climate change was related to functional traits at the leaf level. Authors concluded that with an increase in temperature, species with high LMA and low PS rates (i.e. evergreen species) will be favoured – at least in hot and arid environments, and there will be a consequent shift in the ratio of abundance of evergreen to deciduous species.

In another study with a species from dry tropic ecosystems, Ramírez-Valiente et al. (2017) investigated the intraspecific trait variation of the neotropical oak *Quercus oleoides* in response to natural and experimentally manipulated precipitation regimes in a common garden experiment with five populations. Growth rates, gas exchange and SLA were highly plastic in their responses to the watering treatment. Populations from xeric sites showed higher growth rates than populations from mesic sites during the wet season, demonstrating their resource-acquisitive strategy. Photosynthesis rate per area was positively related to lamina thickness, but negatively to SLA, which in turn was positively related to mass based PS rate, which contradicts results from the global data set by Wright et al. (2004). Similar contrasting responses between populations from the wet and dry end of an aridity gradient were found by Yue et al. (2019) for *Leymus chinensis* in Inner Mongolian grasslands. Under extreme experimental drought applying only one third of growing season precipitation, plant height decreased and $\delta^{13}\text{C}$ as an indicator for water use efficiency increased for the populations from intermediate and low aridity sites. Both plastic responses in functional traits may contribute to increased probability of survival of individuals from less drought affected environments under severely decreasing precipitation under climate change.

The role of plasticity in response to availability of resources (low levels of water and nutrient supply) was studied in a paper for this Special Issue by Diémé et al. (2018) for seedlings of four Sahelian tree species with a wide ecological distribution under controlled environmental conditions in a greenhouse. Species with a high relative growth rate (RGR), i.e. resource-acquisitive species, showed a larger plasticity in their response of RGR, root-shoot-ratio (R/S) and SLA than species with a low RGR (i.e. conservative species). These highly plastic species are also widely spread in Africa and may have a higher capacity to respond to future environmental changes like more severe droughts.

Temme et al. (2018), in this Special Issue, investigated the interaction of soil water availability (SWA) and CO_2 concentration for C3 annuals from past ($160 \mu\text{l l}^{-1}$) to future ($750 \mu\text{l l}^{-1}$) CO_2 concentrations on plant performance and possible trade-offs in growth response to CO_2 and drought, since fluxes of both CO_2 and water are closely linked through stomatal activities, and both CO_2 concentration and SWA affect plant traits such as SLA and biomass allocation (e.g. R/S). For all traits measured, effects of CO_2 and SWA were additive. Thus authors concluded that with more intense drought under global warming, CO_2 fertilization would not counteract effects of reduced SWA.

6. Which traits to choose – from empirical correlations to mechanistic responses

As already discussed above (Section 3), Katz (2018) proposes plant silicon content as a functional trait, both as a response trait (adaptation to stress) and an effect trait (role in ecosystem processes). Similarly, foliar pH has been nominated as a plant functional trait by Liu et al. (2019), in a study on spermatophytes across Northern China, with climate explaining 11% of the variance in foliar pH, decreasing with MAP, but increasing with MAT. Thus, due to its role in many physiological processes (e.g. synthesis of ATP, apoplastic concentration of abscisic acid with relevance for stomatal regulation; Hartung and Slovák, 1991) and in nutrient cycling (e.g. dependence of microbial activities on pH of leaf litter; Bardgett, 2005), foliar pH may also become a relevant response and effect trait under climate change. Other less often studied traits with dependence on climate are defence traits; for instance, oak

species in warmer and drier climates have more condensed tannins, lignin and flavonoids than oak species from colder and wetter climates (Abdala-Roberts et al., 2018).

A plant trait with a well-established relationship to climate and with a clear function for the performance trait biomass is photosynthetic pathway. Plants with C4 metabolism are usually distributed in sunny, warm / hot, dry climates, with Poaceae (grasses) being the dominant family; plants with CAM pathway are abundant in dry environments (but not extremely dry habitats, e.g. Cactaceae and many epiphytes; Keddy, 2017). Thus C4 and CAM plants occur in similar environments, and although they share a number of biochemical features (e.g. phosphoenolpyruvate carboxylase as the initial CO_2 fixing enzyme), a C4/CAM intermediate has been found in one taxon (genus *Portulacca*) until now only. In this Special Issue, Ho et al. (2018) describe a C4/CAM cycling PS pathway for the first time for a (succulent) grass (*Spinifex littoreus*). Due to the adaptive value of both C4 and CAM photosynthesis with respect to high temperatures and low water availability (high water use efficiency in plants of both pathways), both the PS pathway and leaf succulence of *S. littoreus* may be essential traits for minimizing negative effects due to climate warming.

The coordination of plant carbon and water economies is one of the most critical issues in plant adaptation to consequences from climate change such as increased frequency and severity of (extreme) droughts and heat waves. For native species from the Ecuadorian Andes, Chirino et al. (2017) concluded that the link between stomatal behaviour on the one hand and biomass allocation and morphology of the root system (particularly specific root length) on the other hand, is related to drought vulnerability. This demonstrates the need for a physiological balance between the plants' capacity for water uptake and stomatal regulation of water loss.

In a common garden experiment with the South African shrub species *Protea repens* which is distributed over a wide range, stomatal density increased with increasing MAT and drought stress (Carlson et al., 2016). Furthermore, populations from drier and hotter climates displayed higher stomatal density (SD) and conductance and thus transpirational leaf cooling in contrast to wet-site populations. Rates of PS and yield of photosystem II were positively correlated with SD for populations from the hot site only. Thus there was no universal relationship between SD and leaf physiology; rather stomatal density and regulation seem to be an important trait for local adaptation to the hot climate. In another common garden experiment with warming treatment Mediterranean dryland plant species with small leaves achieved higher PS rates than species with large leaves (Valencia et al., 2016). This PS response to simulated climate change can be explained by the effect of leaf boundary layer on transfer of sensible and latent heat as shown by Roth-Nebelsick and Konrad (2018). For the Central Asian riparian forest tree species *Populus euphratica*, Thomas et al. (2017) concluded, based on foliar $\delta^{13}\text{C}$ values, that acclimatization to the local transpiration demand is mediated via SLA.

Although SLA has been considered as a good index for leaf sclerophylly, which may enhance resistance to leaf wilting, Costa-Saura et al. (2016) could not find high correlations between SLA and hydraulic traits such as hydraulic safety margin and resistance to cavitation (PLC_{50}) for woody Mediterranean species along an aridity gradient. Therefore these authors concluded that leaf structure, gas exchange and plant hydraulics act independently. In the two co-occurring Mediterranean oak species *Quercus cerris* and *Qu. pubescens* specific leaf hydraulic conductivity (K_s) was positively correlated to precipitation, and negatively to high temperature (Rita et al., 2016). For increasing frequency or magnitude of extreme climate events, Rita et al. (2016) predict higher reduction of K_s and a greater incidence of xylem dysfunctions. On the other hand, a meta-analysis of the relationship between anatomical xylem traits and environmental variables (e.g. temperature, precipitation, nitrogen deposition) by Borghetti et al. (2017) demonstrated a coordination of xylem traits towards a homeostasis in xylem function as evidenced by an increase of conduit density with

decreasing precipitation and increasing temperature. Similarly, xylem anatomical analysis of ring width, vessel density and mean vessel area for two ecologically contrasting tropical tree species by Islam et al. (2019) showed different adjustment of hydraulic architecture to climate stress. From an extensive study on functional traits of trees as related to drought induced mortality, O'Brien et al. (2017) concluded that physiological parameters such as higher safety margin, resistance to xylem embolism, minimum leaf water potential, leaf-specific conductance, solute concentration, leaf water potential at high vapour pressure deficit (VPD) or low soil water content (SWC) are directly related to tree mortality in most climatic zones, whereas wood density (W_d) as an indirect indicator for resistance to embolism showed positive relationships with tree survival for drought tolerators but not for drought avoiders, and was better correlated with tree mortality in angiosperms than in gymnosperms. Due to the high impact of phylogeny, life history (successional stage, r–K selection) and drought response (deciduous – evergreen, drought tolerators – drought avoiders, isohydric – anisohydric species), O'Brien et al. (2017) concluded that the predictive power of indirect plant traits often used such as W_d is very limited; rather we need a mechanistic understanding based on experimental evidence of physiological drought related traits in order to establish direct links between functional traits and tree mortality due to climatic stress.

Investigating the coordination between leaf and stem functional traits with respect to plant growth strategies, Zeballos et al. (2017) found most of the studied traits to be coordinated at a local scale, probably linked to hydraulic properties, whereas on a global scale this coordination was modified by climatic conditions, being stronger under harsh conditions. At the local scale wood density was negatively related to SLA, with leaf and stem functional traits being generally associated with water use functional traits LA and leaf water potential, i.e. they may be linked to a trade-off between hydraulic conductivity and cavitation resistance. On a global scale, the negative effect size of the correlation SLA– W_d might indicate the trade-off between fast and slow growing strategies. Deepening this multiple-trait method in a meta-analysis applying a more mechanistic approach, Fu and Meinzer (2018) found that water potential at turgor loss point (ψ_{tlp}), which characterizes the coordination between effective stomatal control of plant water status and osmotic properties of leaves, and W_d were related to plant isohydry and anisohydry. More anisohydric species showed lower leaf-specific hydraulic conductivity, greater resistance to embolism and higher W_d . Resistance to embolism via structural reinforcement of xylem seems to be more important than avoidance of embolism via capacity for stem water storage and buffering changes in xylem tension. Apart from these physiological traits related to plant hydraulic architecture, Fu and Meinzer (2018) emphasize the importance of other drought avoidance traits such as safety margin which integrates xylem resistance to embolism and stomatal response to leaf / plant water status which is regulated by multiple physiological processes (e.g. phytohormones such as abscisic acid; e.g. Heilmeyer et al., 2007; Figueiredo-Lima et al., 2018). Furthermore, plant phenology (drought-induced leaf shedding) and below-ground traits (rooting depth and morphology) are of importance for drought resistance.

Root traits like fine root diameter and specific root length (SRL) which are related to plant water relationships, are, according to a meta-analysis by Valverde-Barrantes et al. (2017), related to MAT in coldest parts of species ranges. Although SRL is positively correlated with SLA, the correlation between root and leaf traits is confounded by phylogeny and growth form. Worldwide, MAT is negatively correlated with SRL and positively with fine root diameter, whereas MAP is negatively related to fine root diameter and fine root nitrogen content (Freschet et al., 2017). Thus temperature predominantly affects thickness, whereas precipitation affects chemistry of fine roots. Since these traits respond to soil water and nutrient availability, which in turn may be differentially affected by changing climate parameters, there may be manifold effects of climate change on plant performance and survival.

7. Responses of plant functional traits and vegetation to global warming

There are three major mechanisms how plants can respond to global warming: They may either increase their fitness by (i) acclimatisation via phenotypic plasticity, (ii) adapt to novel constellations of climate factors by heritable genetic variation – both of these trait plasticity mechanisms will allow them to remain at their geographical site –, or they may (iii) migrate to new sites where their trait combination enables them to establish, survive and reproduce.

Different traits have been shown to respond differently to climate parameters, both along environmental gradients and in controlled experiments (cf. Sections 4,5). Thus, under changing climate, depending on novel non-analogue climate constellations, shifts in trait–trait relationships and plant functional types are expected. Based on their analysis of plant trait variation along environmental gradients at the Northern fringe of the Mediterranean Basin, Dalle Fratte et al. (2018) expect more large-leaved species with taller canopies under warmer climate in Southern Europe, i.e. an increase in forest areas at the expense of grasslands, with an increasing proportion of resource-acquisitive and fast-growing species (see also Gillison, 2019b). In contrast, in dry tropical forests, according to Sastry et al. (2018) a temperature increase should favour species with high LMA and low PS rates (at least in hot and arid environments), which causes the relative abundances of evergreen species to be increased at the expense of deciduous species. After three decades of experimental warming in the tundra biome, Björkman et al. (2018) recorded communities of taller plants with more resource-acquisitive leaves, particularly for high soil moisture. Warming caused an intraspecific change in traits, but the shifts in community traits also depended on arrival of novel species from warmer sites. On the other hand, there is also an increase in evergreen dwarf shrubs in the Arctic due to global warming, with ecosystem effects e.g. on litter decomposition and carbon storage being totally different from deciduous shrubs due to contrasting leaf traits (Vowles and Björk, 2019). As for the tundra, soil factors (particularly fertility) interacted with climate across temperate forests studied in New Zealand by Simpson et al. (2016). As a result from modelling MAT, vapour pressure deficit (VPD), soil pH, soil total phosphorus and their interactions, authors predict largest responses of potential vegetation to warming on fertile soils and in wet climates, with species characterized by “fast” leaves (i.e. low LDMC, high SLA and LNC), which in turn will affect plant–soil feedbacks.

With respect to a species' capacity to acclimatize or adapt to the new climate and other environmental conditions at its present site or to migrate to new sites, the position of an individual's habitat with respect to the total species' niche is of high relevance. For the Mediterranean woody species studied along an aridity gradient, Costa-Saura et al. (2016) found that the plants' hydraulic traits were best correlated with the species' optimum niche conditions, whereas the leaf traits were better correlated with the arid limit of the species' niche. Furthermore, there was some complementarity among mechanisms: For the trait combination SLA + safety margin species were at their optimum, whereas the combination SLA + resistance to cavitation characterized maximum aridity, i.e. leaf structure (SLA) and hydraulic traits act independently. Since the environmental limits of species distribution are mainly set by physiological traits determining stress tolerance, Costa-Saura et al. (2016) concluded that prediction of species distribution changes in climate change scenarios will achieve greater robustness and accuracy by including these mechanistically orientated traits and their intraspecific variability.

Usually dynamic global vegetation models (DGVMs) are based on plant functional types (PFTs) with functional traits fixed for a given PFT. Due to various drawbacks of this approach, van Bodegom et al. (2014) based their model of global vegetation distribution on the global distribution of three plant traits (LMA, stem-specific density, seed mass) independent of plant functional or vegetation type. Using the resulting

global trait maps, they could predict global occurrence probabilities of nine representative vegetation types based on their trait combinations with a sensitivity of 42%. Nevertheless, according to the authors the performance of this model may be improved by adding information e.g. on biotic interactions, phylogenetic constraints, disturbance, physiological parameters and additional traits on drought tolerance, dispersal and establishment. Part of these potential improvements had already been considered by Scheiter et al. (2013) in their trait- and individual-based model, incorporating e.g. competition and assigning an individual set of traits such as plant functional type, leaf characteristics and phenology, carbon compartmentation at the whole-plant level and allometry, or resprouting ability to individual plants, thus introducing intraspecific variability.

A similar set of traits different from those quantitative, usually laboratory-measured traits to be extracted from data bases like TRY (Kattge et al., 2011) was used by Gillison (2019b), in this Special Issue, when testing his ‘modal plant functional types’ (PFTs) as possible response indicators for present and future climate. The functional traits used by Gillison (2019b) are related to leaf size, leaf inclination, chlorotype, morphotype, life form and root type. Gillison (2019b) applied either individual traits or modal PFTs constructed from trait combinations either to ‘present’ (1975) or year 2100 climate scenarios, using relationships between plant–climate indicator values (established via empirical plant–climate relationships for five regions covering major biomes) and ten bioclimatic variables. Both modal PFTs and individual traits were highly correlated with bioclimate in both climate scenarios, but modal PFTs were better indicators than single traits. Specific modal PFTs and traits co-vary with regional moisture but to different extents which can be used in predictive modelling. For the year 2100 climate scenario, Gillison (2019b) predicts generally a shift from sclerophyllous, small-leaved shrubby vegetation to fewer hemipterophytes, but more taller woody plants with mesophytic leaves. This kind of vegetation shift is particularly true for the Arctic-Boreal bioclimatic group and corresponds excellently with empirical results from the warming experiments in the tundra by Bjorkman et al. (2018) and Myers-Smith et al. (2019). This demonstrates the predictive power of a modelling approach which does not rely on purely quantitative data accessible only via laborious analytical work performed either in the laboratory (e.g. leaf chemistry, leaf isotope composition, leaf / stem / root hydraulic properties) or in the field (e.g. gas exchange, chlorophyll fluorescence), but on rapid field recording of easily observable functional traits related to resource acquisition and conservation, feasible in all biome types world-wide. As the author emphasizes, rather than using single traits, his approach yields improved functional information about whole-plant fitness when using trait combinations in modal PFTs.

In an analogue approach for the present Special Issue, Box (2019), based on his ‘form follows function’ paradigm, used various plant form types (permanence of above-ground light capturing plant structures, overall plant size, plant architecture including leaf attributes, seasonal activity of plants, below-ground architecture) for an empirical model to predict geographic patterns of richness in plant form and form–function characters. Areas with a high predicted form richness appeared in wet–dry to sub-humid warm regions with relatively long growing seasons. Seasonality (humid and dry seasons, partly also mild winters) appears to be a decisive factor which allows the overlay of deciduous, semi-evergreen and evergreen leaf habits. Box (2019) considers the following potentials for adaptation of plants to climate change: (i) seasonality type, (ii) leaf consistence and size (e.g. SLA), (iii) plant architecture, (iv) plant size, (v) as most conservative: type of leaf or other photosynthetic organ (e.g. green stem; see also Gillison, 2019b).

8. Conclusions

Plant traits are increasingly used to study the adaptation of plants to their environment and to predict effects of environmental change on

plant communities and ecosystems. Partly as a consequence of using standard protocols (Cornelissen et al., 2003; Pérez-Harguindeguy et al., 2013) most studies have centred on a common list of leaf functional traits related to the leaf economic spectrum (Wright et al., 2004). As shown in a number of contributions to this Special Issue, these standard traits are not always clearly correlated to environmental parameters, or their correlations vary between and within species, traits and environments.

Among paleotraits which are commonly used for re-constructing paleoclimate and paleovegetation, single traits such as leaf margin or leaf area have been questioned by Gillison (2019a) as useful indicators for a number of reasons, e.g. taphonomic bias, confounding with other leaf and plant traits or environmental conditions. Additional traits such as leaf venation patterns or leaf mass per area (LMA) have been recommended and successfully applied in a study on Paleogene flora of Central Germany by Kunzmann et al. (2018). Roth-Nebelsick and Konrad (2018) demonstrate that models based on causal mechanisms between leaf traits and environment will help us to understand both the evolution of leaf traits and their adaptive values for past climate and for predicting effects of changing environmental conditions (e.g. atmospheric CO₂ concentrations) on leaves as dependent on various traits such as leaf size or LMA.

A fossil plant trait which has been increasingly used as an indicator for paleoclimate and paleovegetation, based on trait–climate relationship in species (mainly grasses and other spermatophytes) of the extant flora, are phytoliths which can be conserved over millennia in the soil (although the different stability of different phytolith morphs can create problems in interpreting phytolith data in paleoecology; cf. Feng et al., 2017). Nevertheless, they seem to be well-established tools for re-constructing paleovegetation and its interaction with paleoclimate. In this Special Issue, Mukherjee et al. (2018) present the first example of phytoliths from pteridophytes to re-construct paleo-communities along environmental gradients in the Himalaya. Phytoliths represent one aspect of plant silicon (Si) only, and Katz (2018) suggests the use of Si as a response and effect trait e.g. in models of climate change effects on ecosystems.

The study of plant traits along environmental gradients is presently very popular for extant vegetation. However, there are several important confounding factors which can disturb the trait–environment relationships to be investigated, such as phylogeny or growth or life form of the study plants. Following the standard protocols, most studied functional traits are specific leaf area (or its reciprocal value, leaf mass per area), leaf dry matter content respectively leaf water content, leaf nitrogen content and leaf thickness. These traits are not directly related to physiological parameters, rather they represent indicators for leaf anatomy, construction costs or physiology (e.g. resource acquisition and conservation, water relationships and drought resistance). Nevertheless, Dalle Fratte et al. (2018) could find significant relationships between leaf economic traits and soil parameters for more than 1000 plant species studied in Northern Italy. In contrast, in a study on six species along a precipitation gradient in Central Asia, Lang et al. (2018) found trait-specific and species-specific trait–environment relationships for their traits related to aboveground biomass. Using another aridity gradient in Central Asia, Ivanova et al. (2018) studied leaf anatomy of C3 and C4 plants in more detail, such as leaf internal structural and functional parameters like mesophyll structure and composition (chloroplasts), which are directly related to physiological activities such as leaf internal transfer and fixation of CO₂.

Whereas Dalle Fratte et al. (2018) and Ivanova et al. (2018) studied trait variation between species (interspecific variation), Lang et al. (2018) were interested in intraspecific trait variation (ITV). Garnier et al. (2018); Tautenhahn et al. (2019) and Puglielli et al. (2018) investigated ITV with a different aim and study system each. Garnier et al. (2018) assessed the relative contribution of inter- versus intraspecific variation along an aridity gradient and found that trait–environment relationships were partly substantially affected by local disturbance

regimes. Tautenhahn et al. (2019) assessed ITV both in a univariate and a multivariate approach over a large geographical scale, with ITV being more important in the uni- compared to the multivariate approach. In both cases, ITV is due to both heritable genetic variation and phenotypic plasticity. Puglielli et al. (2018) studied phenology as a source of ITV – an important trait in view of climate change with a shift of weather conditions and growing seasons within a given year.

Whereas trait–environment relationships along environmental gradients have to rely on empirical approaches, a mechanistic understanding of trait–environment relationships and causes of ITV is possible in controlled experiments like those by Diémé et al. (2018) under different availability of soil resources on Sahelian tree species and by Temme et al. (2018) under past, present and future CO₂ concentrations for C3 annuals. Physiological mechanisms like photosynthetic pathways are highly relevant for growth and survival – in this context the first report on C4/CAM cycling in a succulent grass by Ho et al. (2018) as an adaptation to hot and dry environments is of high relevance.

Most of the traits discussed above are accessible via costly laboratory measurements only. Although they deliver quantitative continuous data which can be easily transferred to data bases and used in dynamic global vegetation models, they cannot be determined at a large scale for exotic plant and vegetation types covering all relevant biomes. Here, the modal plant functional type approach by Gillison (2019b) represents an alternative, using easily field-observable traits with relevance for resource acquisition and conservation. A major result from the author's modelling exercises using an assembly of traits with higher predictive power than individual traits is an increase of species with resource-acquisitive traits under climate change. Similar conclusions can be drawn from the modelling of Box (2019) who used plant form types in an empirical model to predict geographic patterns of richness in plant form and form–function characters. This increase in fast-growing resource-acquisitive species under climate change conditions agrees with predictions e.g. from Dalle Fratte et al. (2018) and empirical observations by Simpson et al. (2016) and Myers-Smith et al. (2019).

Incorporation of non-quantitative trait information and other data e.g. on historical events, stochastic processes, biotic interactions or phylogenetic constraints into DGVMs have already been suggested by van Bodegom et al. (2014). For example, biotic interactions (e.g. mycorrhiza, nitrogen fixers) can substantially modify trait–environment relationships in various ways (Funk et al., 2016). On the other hand, Yang et al. (2019) recommend consideration of “non-conventional” traits related to basic physiological processes (e.g. carbon isotope values) or drought tolerance (e.g. stem hydraulic properties). The association of traits from the LES with gas exchange may substantially improve climate driven vegetation models (Funk et al., 2016). Even more, traits mechanistically linked to transfer of CO₂ such as stomatal density or mesophyll structure (cf. Ivanova et al., 2018) may even aid in analysis of paleoclimate–trait relationships (cf. Roth-Nebelsick and Konrad, 2018). Hydraulic traits which are directly related to drought resistance (e.g. safety margin, resistance to xylem embolism, leaf-specific conductance, water potential at turgor loss point) have been recommended by O'Brien et al. (2017) and Fu and Meinzer (2018). Furthermore, less common data on leaf phenology and root parameters such as specific root length, diameter of fine roots (Valverde-Barrantes et al., 2017; Freschet et al., 2017) will dramatically improve predictive power of models (see Section 6). Root traits related to plant hydraulics are of special importance in (semi-)arid ecosystems (Funk et al., 2016), the extent of which may increase due to reduced precipitation with climate change in several regions world-wide.

Apart from a more mechanistic approach in selecting functional traits for analyzing both past and future trait–environment relationships (see also Brodribb, 2017), the definition of the driving variables is

most essential. As shown above e.g. for phreatophytes (Salazar et al., 2018) and in a number of other studies, mean annual precipitation is not the critical factor determining soil water availability to plants. Therefore, in the global analysis of Moles et al. (2014), temperature was a better predictor for plant traits, since there is a direct effect of temperature on plant processes, whereas precipitation is only one factor determining soil water content, apart from soil texture, evaporation, soil depth etc. However, mean annual temperature (MAT) does neither yield information on the temperature during the growing season (cf. Tautenhahn et al., 2019), nor on minimum or maximum temperatures (Körner and Hiltbrunner, 2018). Different temperature regimes even with the same MAT will have dramatic effects on plant phenology and tissue damages due to frost or heat stress.

Temperature is particularly important along elevational gradients, which are easily amenable for transplant experiments (cf. Guittar et al., 2016; Henn et al., 2018; Lajoie and Vellend, 2018). Transplant experiments seem highly promising when using complete communities (i.e. soil monoliths, “mesocosms”), since this maintains the potential for biotic interactions including plant–soil feedbacks (Niedrist et al., 2016). Transplant experiments can be performed with contrasting or similar species composition of study communities. In the latter case, the relevance of intraspecific variation and its components (heritable genetic variation, phenotypic plasticity or phenology) can be assessed – a vital pre-requisite for assessing the potential of fast plastic trait responses with limited scope versus slow adaptive evolution processes with a broad scope (Siefert et al., 2015).

Traits usually less considered are those related to regeneration (dispersal / colonization, germination, emergence, resprouting). These regenerative traits are particularly important in case of disturbances (Funk et al., 2016) and – in case neither plasticity nor adaptive evolution will allow a plant to survive in its habitat in view of drastic environmental changes – for migration to new habitats, as has been predicted for example by climate niche modelling for six oak species occurring in Baja California (Mexico) under scenarios of global warming by Ramírez-Preciado et al. (2019). Therefore regenerative traits should be incorporated in DGVMs as well (see Scheiter et al., 2013).

Another topic often neglected when analysing trait–environment relationships is phylogenetic relatedness (but see Wigley et al., 2016; O'Brien et al., 2017; Valverde-Barrantes et al., 2017; Šimová et al., 2018; Yang et al., 2019). In the study of Yang et al. (2019) with 483 species on 48 sites in China from seven different vegetation types, family alone accounted for 17% of total trait variance, and together with climate 29%. The phylogenetic effect was particularly strong for LDMC, less so for SLA, since LDMC depends more on genetically controlled leaf structural properties than SLA.

Leaf properties such as LMA but also the presence of chemical compounds (e.g. chlorophyll, lignin and phenols) can now be detected via remote sensing (RS) over large scales (cf. Asner et al., 2017). Other plant traits amenable to RS estimation are leaf phenology, and plant height and architecture via airborne laser scanning (Zlinszky et al., 2015). This opens new perspectives not only for monitoring vegetation changes due to climate change, but also the window for mechanistic analysis of underlying trends from regional to continental scales (see also Box 1).

The question how trait–environment relationships will be affected by trade-offs and associations between traits, by species capacities for trait acclimatisation and adaptation, and by phylogenetic constraints under novel, non-analogue climate will be a major challenge both for scientists and for plants struggling for survival in a world with unprecedented anthropogenic environmental changes.

Box 1

Perspectives for future research on functional plant traits – climate change relationships.

| Research field / Study question | Specific topics / possible approach |
|--|--|
| <i>Climate parameters</i> | Clear definition e.g. of “water availability” (different from mean annual precipitation!) and physiologically relevant temperature (different from mean annual temperature!) |
| <i>Mechanistic plant traits</i> | Traits related to physiological processes, e.g. leaf carbon isotope data, stomatal density, leaf internal anatomy, gas and water exchange, leaf / stem / root hydraulic properties, stem / root anatomy, fine root diameter, rooting depth, root system architecture |
| <i>Intraspecific trait variation (ITV)</i> | Different scales (within / between individuals, plot / site, population, landscape), ontogeny + phenology |
| <i>Disturbances</i> | Regenerative traits (dispersal / colonization, germination, emergence, resprouting) |
| <i>Transplant experiments</i> | Use of complete communities including soil environment (mesocosms) |
| <i>Remote sensing</i> | Hyperspectral imaging: Leaf structural traits (LMA), leaf chemistry (e.g. chlorophyll, lignin and phenols) |
| <i>Modelling</i> | LIDAR: plant height, plant architecture, leaf phenology Biotic interactions, local environmental conditions (soil, microclimate), ITV, physiological parameters, drought and temperature tolerance, dispersal and establishment processes |

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